ABUNDANCE AND FEEDING PREFERENCES OF FLY LARVAE IN TWO WOODLAND SOILS

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INTRODUCTION

The larvae of Diptera are a prominent component of the soil fauna but as a result of extraction and taxonomic problems they have been neglected by soil zoologists. General accounts of our fragmentary knowledge of the biology of soil-living fly larvae are given by KUHNELT (1961), BRAUNS (1954) and RAW (1967), and HENNIG, (1948, 1950, 1952) gives much information on the general biology of dipterous larvae. No comprehensive studies of woodland populations have been made, but those of VAN DER DRIFT (1951), SZABO *et al.* (1967) and FREEMAN (1967) include much useful information. This account describes work preliminary to a study of energy-flow and production by populations of fly larvae and gives a description of the abundance and feeding preferences of the fauna of two woodland soils.

We have developed an extraction technique (HEALEY and RUSSELL-SMITH, 1970) that appears to give an adequate assessment of population. Very many taxonomic difficulties remain but are gradually being solved by extensive culturing of larvae through to the adult stage, in which they can be identified by specialists. The soils studied are a well-developed mull in mixed deciduous oak woodland on Carboniferous limestone in northern Lancashire and a moder in coppiced beech woodland on London Clay in Kent. The features of the two soils are summarized in Table 1.

METHODS

Each month during 1968 and 1969 24-30 soil samples (25 cm^2 × 6 cm) were taken from both the mull and moder soils. The litter and humus layers were separated and after storage for up to one week at 2°C fly larvae were extracted by a technique involving sieving of the soil and flotation in a glycerol/water mixture (HEALEY and RUSSELL-SMITH, 1970). Larvae were preserved in 70 p. 100 ethyl alcohol. With some exceptions it has been possible to identify fly larvae only to family level.

For the analysis of gut contents individuals were selected at random from the samples. Small

TABLE I

	Moder	Mull
Site	Blean Woods National Nature Reserve, Kent.	Meathop Wood, Lancashire.
Vegetation	Canopy of coppiced beech (*Fagus sylvatica* L.) with some sweet chestnut (*Castanea sativa* MILL.), oak (*Quercus petraea* (MATTUSHKA) LIEBL.) and birch (*Betula pendula* ROTH.). No ground flora.	Canopy of oak (*Quercus petraea* (MATTUSHKA) LIEBL. with ash (*Fraxinus excelsior* L.) and birch (*Betula pendula* ROTH.) and an understorey of coppiced hazel (*Corylus avellana* L.). Ground flora dominated by *Rubus fruticosus* L. agg., *Endymion nonscriptus* (L.) LARCKE, *Anemone nemorosa* L., *Mercurialis perennis* L. and *Oxalis acetosella* L.
Soil	An oligotrophic brown earth on London clay with a moder humus type. Depth of horizons: litter (A0 and AL1) 1-3 cms; humus (AL2, AH1 and AH2) 3-4 cms, clay (B horizons) below 5-7 cms. pH of horizons A0 and AL1 4.1-5.7, mean 5.0; AL2 and AH2 3.1-4.5, mean 3.9; B 3.4-4.6, mean 3.9.	A brown earth on Carboniferous limestone with a mull humus type. Depth of horizons: litter (A0 and AL1) 0-1 cm; humus (AH layers) 5-6 cms; clay (B horizon) below 6-7 cms. pH of horizons: litter no information available, humus (about 5 cms depth) 4.1-7.3, mean 5.3.
Litter production	About 360 g/m² year. Composition: beech 70 %, chestnut 10 %, oak and birch 20 %.	377 gm²year. Composition : oak 42 %, ash 25 %, hazel 13 %, birch 12 %.
Rainfall	Mean annual rainfall 60-70 cms. Peak rainfall in October and November.	Mean annual rainfall 120-125 cm. Peak rainfall in July, August, November and December.
Temperature	Mean soil temperature (AH1 layer) 1967 about 12.1 °C.	Mean soil temperature (AH layer) 1967 8.3 °C.

larvae were cleaned in warm lactophenol, squashed onto a slide and mounted in Gurr's A. C. S. Mountant. The guts of larger larvae were removed by dissection and opened before squashing and mounting. Gut contents were examined by phase-contrast microscopy and the proportion of different food components in the gut was estimated visually. Many valid criticisms can be made of gut contents analysis as a method for defining food preferences. For instance, many species take into the gut material which they do not use as food (e. g. soil mineral particles in the case of many soil animals) and the differential rates of digestion of food materials often give a misleading impression of the relative importance of components (e. g. REYNOLDSON and YOUNG, 1963). But few other simple methods for studying the food preferences of small arthropods are available, and analysis of gut contents was thought adequate to define broad feeding categories within the Diptera. Similarly more quantitative methods of analysis were not felt to be justified at this stage. An additional criticism of the present study is the cold storage of the soil samples before extraction of the larvae. Experience of this work, and also with Collembola (HEALEY, in prep.) suggests, however, that there are no obvious differences in the appearance of gut contents of cold-stored animals and those collected in the field. Whenever possible apparent food preferences have been confirmed by observation of feeding behaviour in the field and the laboratory. More intensive studies of the feeding of some particular species are in progress.

RESULTS

Feeding preferences

The fly larvae will be considered in two groups, those that are predominantly litter dwelling forms and those that are restricted to the humus. For the purposes of this paper the litter layers include the A_0 and A_{F_1} horizons and the humus layers include horizons A_{F_2}, A_{H_1} and A_{H_2}.

1. *Litter dwelling forms.*

Phoridae. — The guts of Phorids contained a finely-divided mass of fungal hyphae, fungal spores, coccoid algal cells, pollen, testate amœbae and fine humic material (figs 1 A and B). Observations in the field revealed that this group feeds by scraping the surface of moist, undecomposed leaves in the A_0 layer. The food was therefore likely to consist both of fungi, algae and bacteria growing on the leaf surface and of the faeces of other organisms which have been deposited there.

Lonchopteridae (*Lonchoptera lutea* PANZER). — The gut contents of this species were very similar to those of the *Phoridae* but more finely divided and with a smaller proportion of fungal hyphae and testate amœbae. While direct observation of feeding was difficult in this species, since the mouth-parts lie beneath the body, it seemed likely to be a leaf-surface scraper with somewhat smaller mouthparts than those of phorids.

Ceratopogonidae (*Forcipomyia* sp.) — The gut contents consisted of very finely divided humic material with fungal hyphae and a large proportion of fungal spores. In the absence of more quantitative data it was not clear whether they are generalized leaf scrapers or more specialized fungal feeders.

Mycetophilidae (*Phorodonta flavipes* MG.). In 1968 field and laboratory observation showed this species to feed extensively on slightly decomposed beech litter, an interpretation which was confirmed by examination of gut contents which consisted of large fragments of beech leaf and some fungal hyphae. In 1969, however, examination of gut contents showed typical leaf surface material (such as was found in phorid guts), an apparent change in feeding habit that requires further investigation.

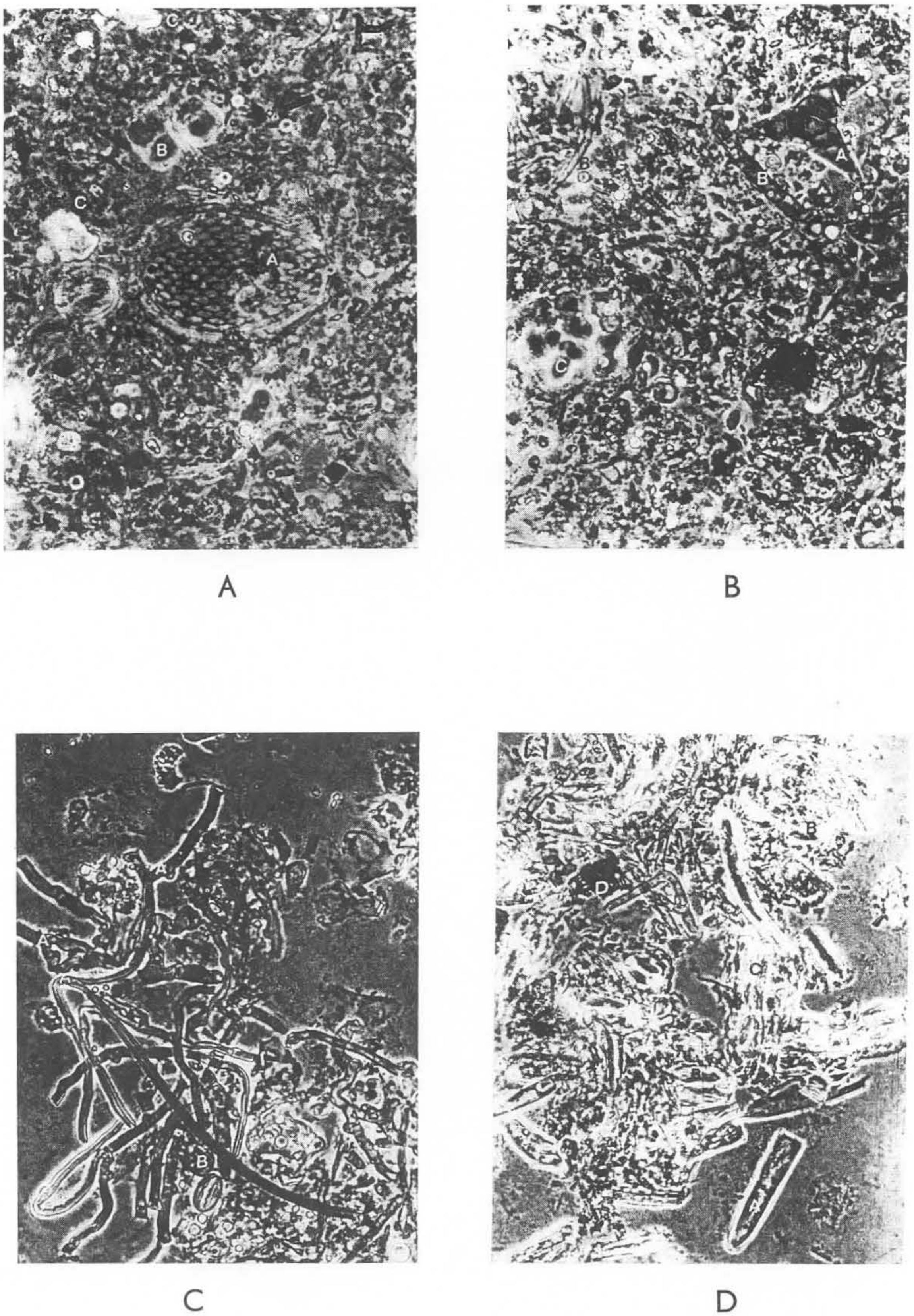

FIG. 1. — A. *Gut contents of phorid larva* (× 480) *showing* (a) *shell of testate amoeba*, (b) *coccoid algal cells* (c) *small mineral particles*
B. *Gut contents of phorid larva* (× 460) *showing* (a) *fungal spore*, (b) *fungal hyphae*, (c) *coccoid algal cells*
C. *Gut contents of sciarid species* (× 460) *showing* (a) *basidiomycete hyphae*, (b) *pollen grain*.
D. *Gut contents of sciarid species* (× 460) *showing* (a) *hair cell from plant*, (b) *stomacal cells*, (c) *pa*[illegible]*chyma* (?) *cells*, (d) *fragment of fungal sclerotium*, (d) *basidiomycete hyphae*.

Humus living forms.

Cecidomyidae (*Lestremiinae*). — All larvae of this sub-family are free living forms, none of which are known to be gall makers. Examination of an extensive series of larvae from both soils failed to reveal any gut contents. All the individuals examined, however, possessed mouthparts which appeared to be adapted for piercing with sharp stylet-like mandibles (HENNIG, 1948, p. 115). It is tentatively suggestedthat cecidomyids may in fact feed by sucking the contents either of fungal hyphae or of fine roots. Further research is needed on feeding in this group which forms a large component of the fauna of the moder soil in Blean Woods.

Mycetophilidae. — Sciarid larvae formed an important component of the total larvae on both sites. Gut contents included a large proportion of plant cells (including epidermis and stomata), fungal hyphae and spores, pollen grains, fine humic material and mineral grains (fig. 1 C and D). Although sciarids were clearly fairly general humus feeders, differences in gut contents could be detected between samples from the two sites, reflecting the different availability of the various food components in the two soils. On the moder soil at Blean a high proportion of basidiomycete hyphae were observed in the guts but these were absent from samples taken from the mull soil at Meathop. Conversely those from the mull soil contained a much higher proportion of mineral particles which was probably due to the greater degree of mixing that took place.

Chironomidae (*Smittia curticosta* EDWARDS). — This terrestrial chironomid formed between 45 p. 100 and 55 p. 100 of the total fly larval fauna in the Meathop soil but was totally absent from Blean. Unlike other chironomids 40-100 p 100 of all animals examined had full guts, indicating that this species probably feeds continuously (fig. 2 A). The gut contents consisted almost entirely of very finely divided humus material and abundant mineral particles with occasional fragments of fungal hyphae (fig. 2 B). The absence of many of the food components found in sciarid larvae and the low average particle size suggested that this form is a selective humus feeder. It is not yet established, however, whether it assimilates free organic matter or whether it digests and assimilates bacteria adhering to the soil particles.

Other chironomids (*Orthocladiinae*). — Chironomids other than *S. curticosta* were abundant in both soils. By contrast only a proportion of these larvae had gut contents. For example, a sample taken from the moder soil in December 1969 showed only 54 p. 100 of 118 individuals to have gut contents. The nature of the gut contents was related to the position in the soil profile from which they had been collected. Samples from the litter layer on the moder soil had gut contents similar to those of *Phoridae* but with less fungal hyphae and a higher proportion of fine humic material. Samples from humus showed a similar gut content composition to sciarid larvae but with a smaller range of particle sizes.

Dolichopodidae and Empididae. — At least 50 p. 100 of all dolichopodids and empidids examined on both sites showed no gut contents detectable by the methods used. Of the remainder the majority showed enchytraeid chaetae alone or enchytraeid chaetae in association with humus (fig. 2 D). From Meathop two large individuals were examined, one of which contained a complete sciarid larvae and the other a complete larvae of *Smittia curticosta* (fig. 2 C). While it was not clear whether the enchytraeids were taken alive or not, it would appear likely that the fly larvae were,

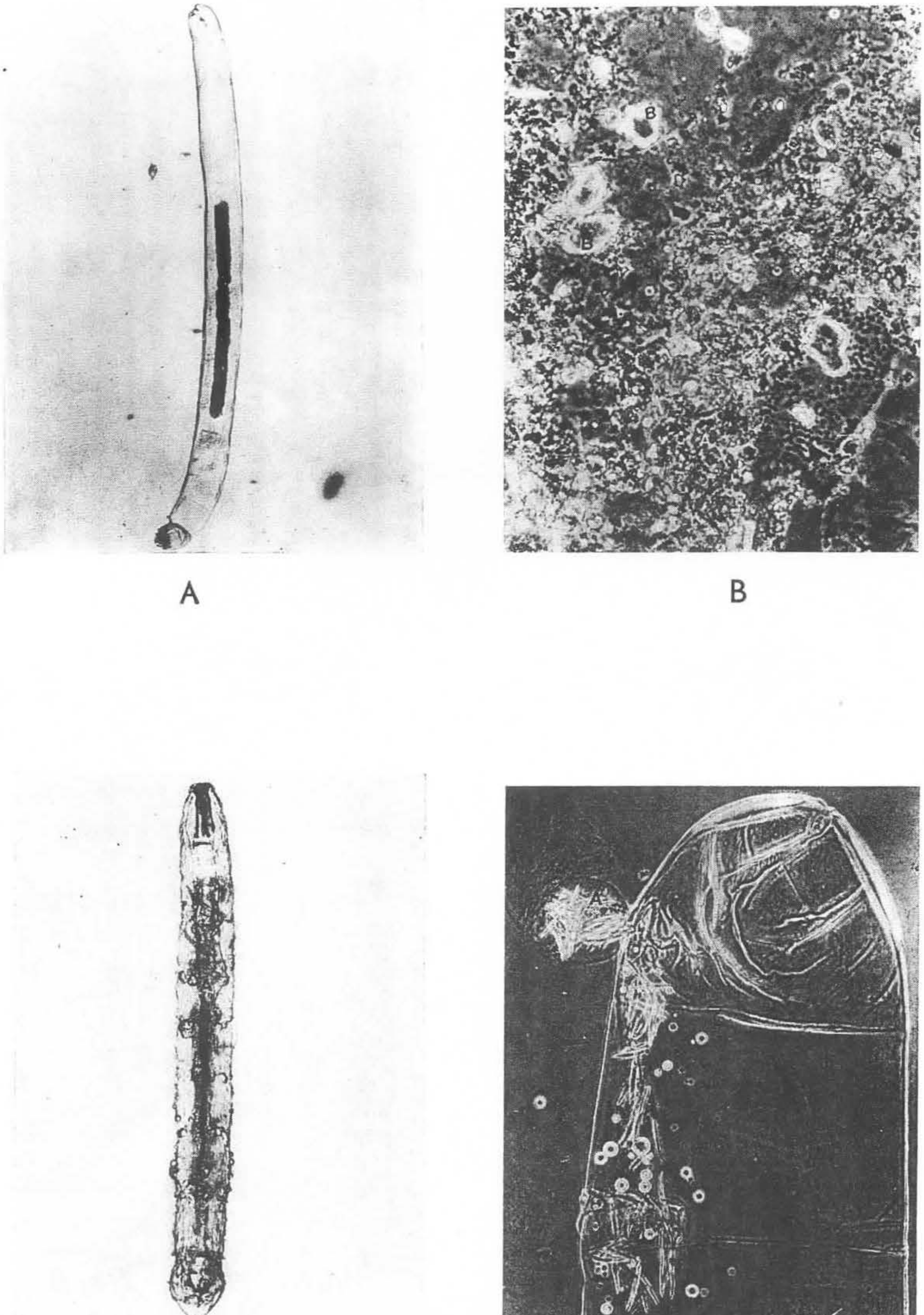

FIG. 2. — A. *Larva of* Smittia curticosta (× 110) *cleared in lactophenol to show gut contents*
B. *Gut contents of* S. curticosta (× 110) *showing* (a) *finely divided humic material*, (b) *mineral particles*.
C. *Dolichopodid larva* (× 40) *cleared in lactophenol to show larva of* S. curticosta *in gut* (a-b).
D. *Dolichopodid larva* (× 200) *showing Enchytraeid Chaetae* (a) *in gut and extruding from anus.*

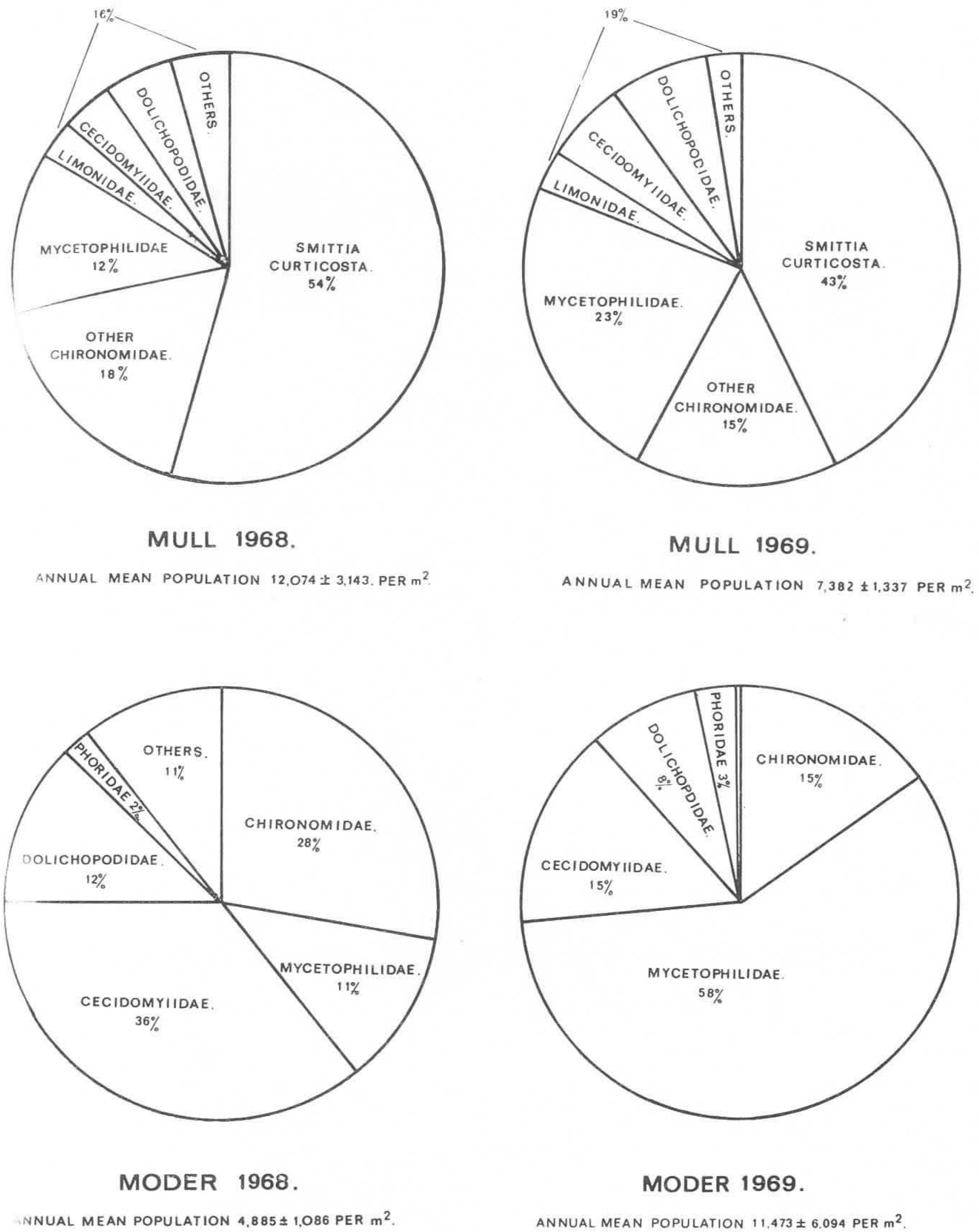

FIG. 3. — *The proportional representation of some groups of fly larvae in the annual mean populations in mull and moder soils in 1968 and 1699 The mean populations are given, with their 95 per cent confidence limits.*

since both retained their form and gut contents. Further study is required to establish whether or not the larvae of these families are solely predators.

Abundance

Figure 3 shows the proportions of the annual mean populations in the mull and the moder made up by the most important families of fly larvae, and figure 4 shows how these were distributed between the litter and humus horizons. Confidence limits for the mean populations are wide because of great fluctuations in the size of the population through the year. In the mull in 1968, for instance, populations ranged from a peak of 23 000, with 95 p. 100 confidence limits of 5,800 in March to a minimum of 6 300, with 95 p. 100 limits of 900, in August. There was considerable variation in abundance in the two soils and between the two years and this will be the subject of a further paper. In general, numbers of fly larvae were highest between February and April and lowest, after emergence of adults in late summer, and this pattern was found in both soils. In 1968 the mull had consistently higher populations than the moder, but in 1969 very large populations of a mycetophilid (*Sciara* sp.) were present in the moder, so that the annual mean population (which has very wide confidence limits) was much higher than in 1968. Larvae belonging to 16 families have been found in the moder and 13 in the mull, and there are indications that specific diversity may be much greater in the moder.

In the mull soil incorporation of leaf litter into the A_{H_1} horizon was very rapid and the litter horizon was thin and diffuse, except in the late autumn and winter. Therefore very few larvae were recorded from the raw litter horizons. A very high proportion of the population here consisted of the larvae of the chironomid *Smittia curticosta* and this and other species of chironomid accounted for 72 p. 100 of the population in 1968 and 58 p. 100 in 1969. Over 98 p. 100 of the *S. curticosta* larvae and 80 p. 100 of the other chironomid larvae occurred in the humus horizons. There was a very marked seasonal variation in the proportion of chironomid larvae in the litter layers. In April 1968 all larvae were found in the humus while in November of the same year 82 p. 100 were in the litter layers. This pattern of spring populations predominantly in the humus and autumn populations predominantly in the litter was repeated in 1969. *Mycetophilidae* (of which there was probably a single major species, *Sciara* c. f. *autumnalis* WINN.) was the only other abundant group and these, too, occurred almost entirely in the humus layers. The *Dolichopodidae* (this category may also include some *Empididae* which cannot at present be separated as larvae) are probably partially predatory and are also found in the humus horizons.

In the moder, litter and fermentation horizons up to at least 1 cm depth are present all through the year. A much higher proportion of the fly larval fauna (27 p. 100 in 1968 and 17 p. 100 in 1969) was found in the litter here than in the mull. *Chironomidae* were much less prominent than in the mull ; there were several species of *Orthocladinae*, none of which was clearly dominant. In 1968 around 40 p. 100 of these were found in the litter, but in 1969 (a drier year) the proportion was much lower. *Cecidomyidae* of the free living *Lestrimiinae* were the most abundant larvae in 1968, and about 35 p. 100 of these were found in the litter. In 1969 *Mycetophilidae* were much more abundant and accounted for over half of the mean annual popula-

n and about 15 p. 100 of these were found in the litter layer. The *Phoridae*, which re shown to feed by scraping the surface of leaves, were found almost exclusively in the litter layer.

DISCUSSION

The feeding relationships of the organisms of the decomposer food web are proving one of the most intractable of ecological problems. In contrast to the herbivore web, the decomposer web seems to contain few forms with specialized diet, so that the feeding habits of many different species often appear similar. It is possible that this uniformity of feeding may be more apparent than real and that detailed studies of individual species may reveal distinct preferences for food substrates, or at least varying abilities to digest materials from apparently uniform substrates (NIELSEN, 1962). Despite working mostly at the family level of classification of fly larvae and using only gut contents analysis and observations of feeding behaviour we have been able to distinguish distinct types of feeding activity and to relate these to the places where the larvae were found. Feeding preferences of particular families were similar in the two different soils. but showed small differences that could be related to the structure and components of the two humus types. In general our conclusions about the feeding habits of the families agree with those noted by other workers.

STRENZKE (1950) recorded terrestrial chironomid larvae as having gut contents containing fungal hyphae and spores, diatoms, fragmented plant remains and amorphous detritus. Although we found no diatoms, this is very similar to the gut contents of our species and it seems that these are unselective humus feeders. Chironomids collected from the litter layer of the moder, however, appeared to be feeding on the surfaces of leaves and the fungal and detritus material associated with them. RAW (1967) notes sciarid species (*Mycetophilidae*) as fungal feeders, whilst KUHNELT (1961) and BRAUNS (1954) indicate broader preferences for decomposing leaf material. Our species appeared to be rather general humus feeders with one, *Phorodonta flavipes*, feeding on slightly decomposed beech leaves. Soil-living *Cecidomyidae* are said by RAW to feed on faeces, but BRAUNS noted them as feeders on fungal material: we have as yet obtained no indication of the diet of our species. Many species of *Phoridae* are known to be parasitic on other invertebrates and RAW states that others are necrophagous forms. The phorids found in the moder in this study appeared to feed by scraping the surface of leaves in the early stages of colonisation by microorganisms. HENNING (1952) considered the *Dolichopodidae* to be largely predators of small insects, including fly larvae and Collembola and aquatic species are noted by BROCK *et al.* (1969) as predators of the eggs and larvae of other Diptera. Although many of our *Dolichopodidae* contained no gut contents we found evidence of predation on fly larvae in the mull and *Enchytraidae* in the moder, although the latter could have been taken after death. The guts also contained humus but whether this is a regular component of the diet or is derived from the gut contents of prey is not known.

The levels of abundance of fly larvae that we record are high compared with earlier studies. This is related to the high efficiency of our extraction technique (HEALEY and RUSSELL-SMITH, 1970). Most earlier population estimates (e. g. VAN

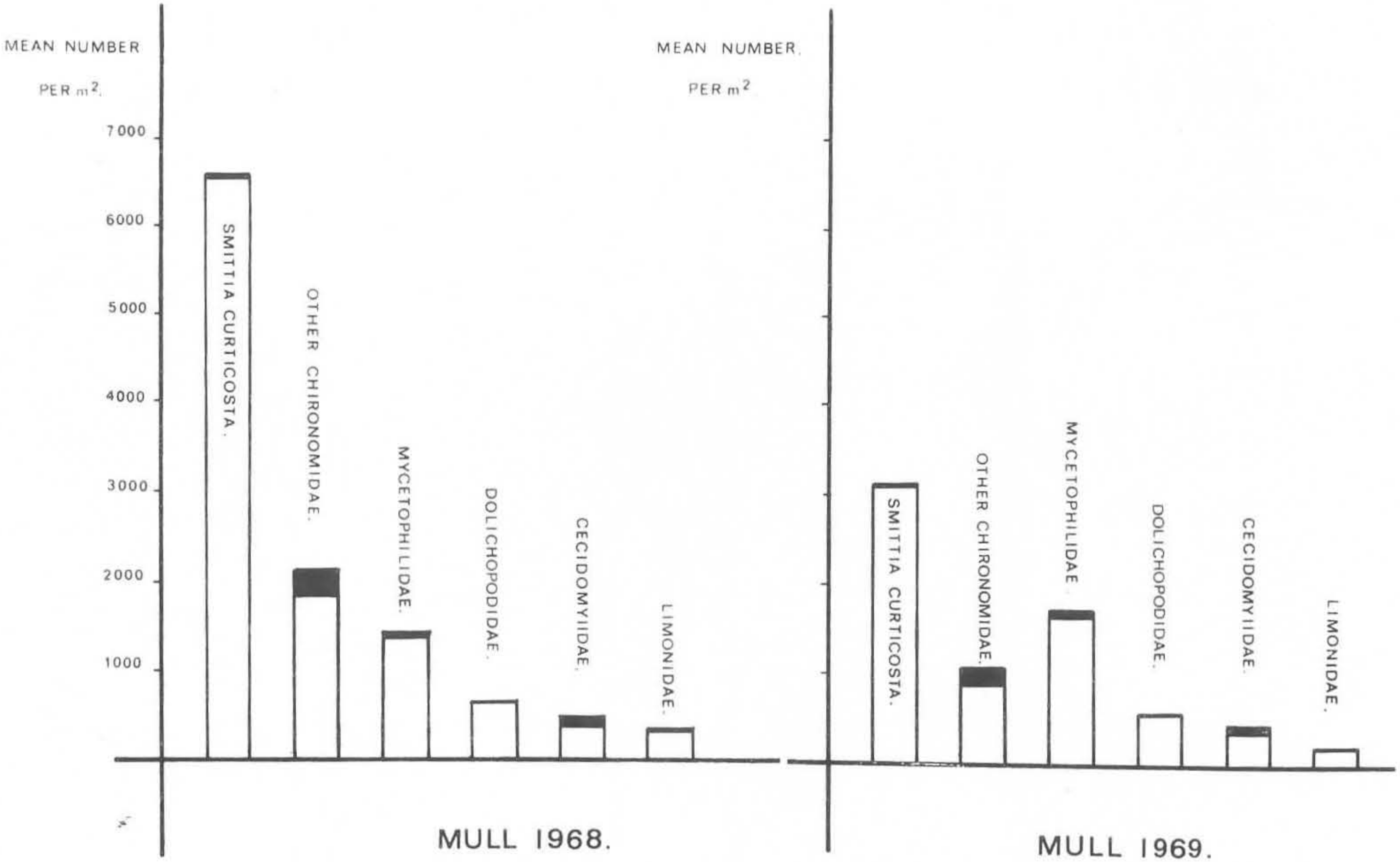
MEAN NUMBER
PER m2.
7000
6000
5000
4000
3000
2000
1000
SMITTIA CURTICOSTA.
OTHER CHIRONOMIDAE.
MYCETOPHILIDAE.
DOLICHOPODIDAE.
CECIDOMYIIDAE.
LIMONIDAE.
MULL 1968.
MEAN NUMBER.
PER m2
SMITTIA CURTICOSTA.
OTHER CHIRONOMIDAE.
MYCETOPHILIDAE
DOLICHOPODIDAE.
CECIDOMYIIDAE.
LIMONIDAE.
MULL 1969.

FIG. 4.

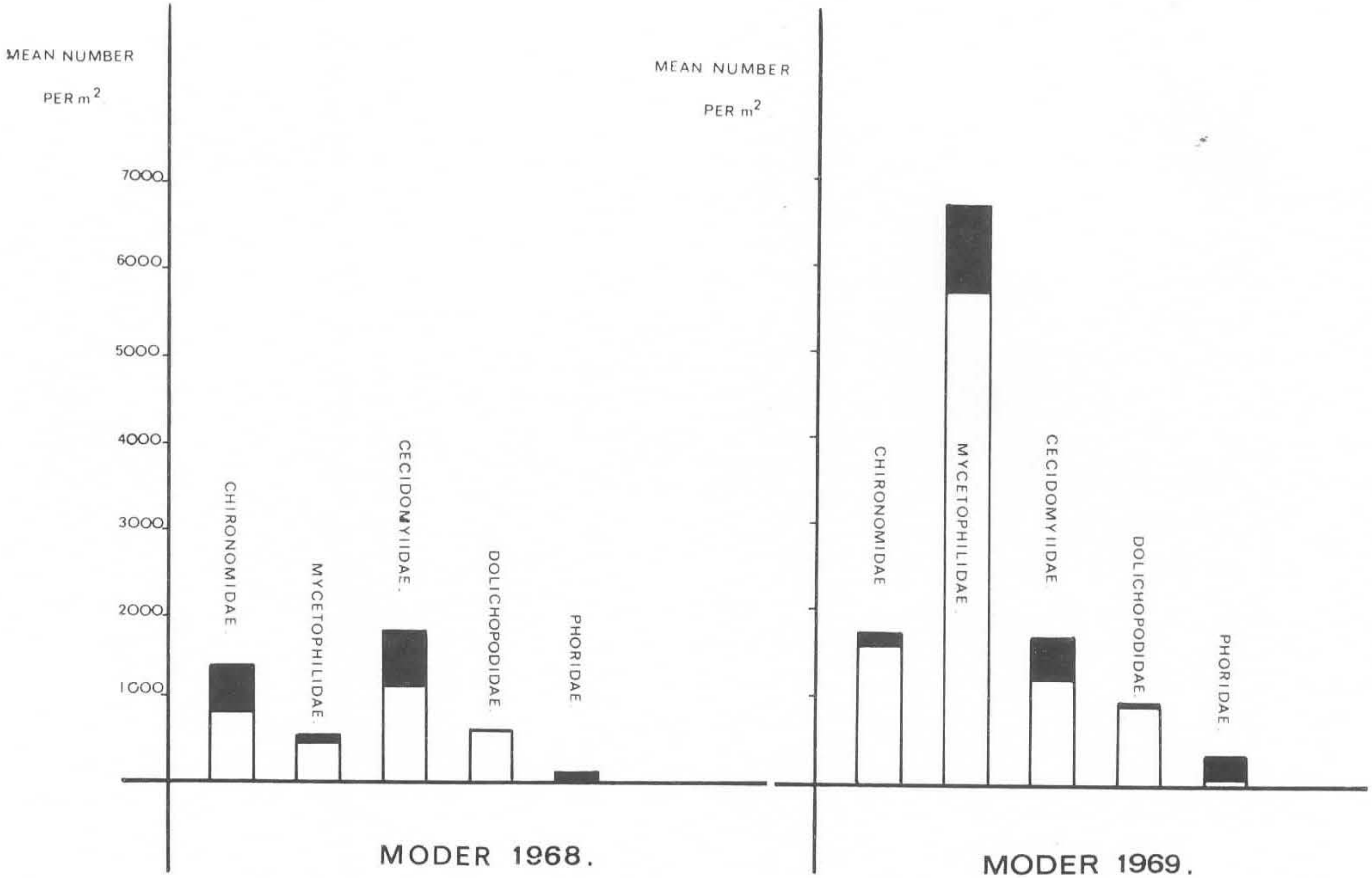

FIG. 4. — *The number of fly larvae of various groups comprising the annual mean populations nimull and moder in 1968 and 1969. The black portions of the histograms represent the numbers of the population occupying the litter and humus horizons*

DER DRIFT, 1951) have been derived from Tullgren funnel extractions. We have shown that simple Tullgrens extract only about 12 p. 100 and the high gradient extractor (MACFADYEN, 1961) about 26 p. 100 on the fly larvae in a moder soil. Conventional flotation techniques (RAW, 1957) also have limited success with fly larvae. It is not surprising therefore that our estimates are 6-10 times those from earlier studies of woodland populations and that our samples contain more small forms.

Comparisons of abundance of fly larvae in the mull and moder are distorted by the very high numbers of a species of *Sciara* in the moder for a few weeks in the autumn of 1969 and not noted the previous year. If this apparently transitory phenomenon is excluded, for the greater part of the year the populations in mull were over twice those of the moder. The structure of the moder was more complex than the mull, with more available microhabitats, so that the distribution of fly larvae was more complex. A much higher proportion of the population lived in the litter horizons and there are indications that, despite lower abundance, specific diversity is greater in the moder than the mull.

The most distinct difference between the soils is that *Chironomidae* maintain an average density over two years of 6, 500 per m² in the mull and only 1, 500 in the moder. Terrestrial chironomid larvae generally have fewer protuberances and appendages than aquatic forms, but otherwise it is not known what special adaptations they have for terrestrial life. KUHNELT (1961) states that *Chironomidae* are frequently abundant in the leaf litter of moist beech forest, but other studies (e. g. STRENZKE, 1950) emphasise their abundance in rather wet soils. During the present study the new autumn generation of *S. curticosta* in the mull was much slower in establishing itself after the dry summer of 1969 than in the previous year, and numbers have continued to be low through the winter of 1969-70. This may be evidence of the susceptibility of terrestrial chironomids to drought. Rainfall in the mull is about twice that in the moder on average, but the mull has much freer drainage so that it becomes waterlogged less. Nevertheless, taking both rainfall and soil structure into account it is likely that there is a more even distribution of moisture in the mull profile than the moder and this may be a factor favouring the *Chironomidae*. Others may be that the uniform structure of mull and the absence of abundant fibrous material may be more suitable for movement of small limbless larvae lacking skeletal structures. It also seems possible that the finely-divided, evenly-distributed humic material of the mull profile may be very suitable for the feeding of forms like the *Chironomidae*, which apparently feed by « eating their way » unselectively through the soil. If such forms digest free amino acids or bacteria they are likely to be favoured by the high concentration of these in mull.

The remaining contrasts in the fly fauna of the two soils are the greater abundance of *Cecidomyidae* in the moder, for which we have no explanation, and the prominence of *Phoridae* in the moder, which is related to their litter-feeding habit. *Limonidae*, which are mainly humus feeders, are present in small numbers in the mull humus but are absent in the moder.

One surprising feature of these soils is the relative absence of large humifying forms such as *Bibionidae* and *Tipulidae* which are common in grassland and moorland (COULSON, 1962) and certain types of woodland (FREEMAN, 1967 ; SZABO *et al.*, 1967). We have found a small number of bibionid larvae in the moder at Blean Woods, an

in the early summer adults are commonly seen in flight, but for the most part the larvae must live in specialized microhabitats not covered by the present sampling programme. *Tipulidae* are found occasionally in the mull but most of the population lives in restricted microhabitats such as rotting wood, under stones, in moss hummocks, etc.

The role of a group of animals in soil processes cannot be judged from estimates of numerical abundance but only from an assessment of their contribution to energy flow. Work on production and energy flow in some of the major species of fly larvae in both the mull and moder soil is in progress, but it is already clear that biomass estimates may give a different impression of the relative contributions of the families in the two soils. The larvae of *S. curticosta*, for instance, are numerous but small. They have a mean weight of 45 ± S. E. 3.5 μg, so that it is unlikely that annual mean biomass in the mull exceeded 0.30 g in 1968 and 0.15 g in 1969. The biomass of this species is therefore comparable with that of the total Collembola in many soils (HEALEY, 1970). The biomass of *S. curticosta* may be less than that of the *Mycetophilidae* which are less numerous but larger. Similarly the great abundance of large mycetophilids in the moder in 1969 may indicate a much higher biomass compared with the previous year or with the mull than the estimates of numerical abundance alone would suggest.

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RÉSUMÉ

ABONDANCE ET PRÉFÉRENCES ALIMENTAIRES DES LARVES DE DIPTÈRES DANS DEUX SOLS FORESTIERS

On a décrit d'une façon générale les niveaux d'abondance et les préférences alimentaires de larves de diptères dans deux sols forestiers, un mull et un moder. La moyenne de la population dans le mull était 12 050 ± S. E. 1,600 par m² en 1968 et 7 380 ± S. E. 680 par m² en 1969. Les *Chironomidae* terrestres, qui se nourrissent d'humus, y étaient dominants. La moyenne de cette population dans le moder était 4 880 ± S. E. 550 par m² en 1968 et 11 470 ± S. E. 3,100 par m² en 1969. Les *Mycetophilidae* et les *Cecidomyidae* y étaient dominants. On a pu définir des préférences alimentaires distinctes dans différentes familles et, dans certains cas, dans différentes espèces. Ces préférences se rapportent, d'une façon générale, au type d'humus.

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DISCUSSION

G. MARCUZZI : Asks whether Dr HEALEY has determined the water content of the soils he has studied, since he thinks that the different Diptera larvae composition can depend on the different water conditions of mull, compared with moder, mull in general is more humid than moder.

I. N. HEALEY : The mull receives nearly twice as much rainfall as the moder but drains more freely, so, curiously, is frequently drier. But I agree with Professor MARCUZZI that the moisture status of the soils is probably a major factor in determining the composition of the fly larval community.

P. J. A. HOWARD : To enlarge upon Dr HEALEY's reply, earlier this year I sampled the mull soil with a cover and even after some days of rain the mull soil was dry enough to crumble and fall out of the cover. On the other hand, as Dr Healey suggests, the high organic content of the moder probably gives it a much greater water retention.

M. S. GHILAROV : Probably the connection of *Smittia* larvae with mull mentioned by Dr HEALEY is characteristic of humid climatic conditions. In more continental ones these larvae inhabit « moder », « rough humus », but not mull, which is forming in drier conditions due to the activity of such invertebrates as earthworms, the latter being absent in wet soils inhabited by Chironomid larvae.

G. ZACHARIAE : You differentiate between scraping of the microbial surface film and feeding on cell material. But in well decomposing leaf species don't the scrapers eat weakened cell material too, especially from the morphological underside, if the consistency lies within the range of mechanical selection by the larva So there were not strong limits in this respect. Or did you observe any chemical or behavioural distinction in at least certain groups ?

A. RUSSELL-SMITH : We have not observed plant cell material in the gut contents of these larvae. Scraping forms we have studied. However beech and oak leaves have relatively hard cuticles and it may be that if they were feeding on softer leaves, such as hazel or hornbeam, they might ingest leaf material as well. However we have no observations as yet on behaviour.

G. J. F. PUGH : The numbers of toadstools can vary very greatly from one year to another, but little is known of variations in the amount of their hyphae in the soil and in the litter layers. The great upsurge of mycelium feeding larvae in one autumn may reflect a good year for the growth of basidiomycetes, and it would be interesting to compare fluctuations in numbers of these larvae with the quantity of toadstools in different years.

M. J. SWIFT : Whilst there is no direct evidence linking hyphal abundance and abundance of sporophores in agarics, we might presume that as sporophore production requires the mobili

tion of organic material from the substrate, sporophore abundance will probably be correlated with hyphal activity.

P. W. MURPHY : The differences in numbers of larvae in each year is a striking feature of this study. Could Dr HEALEY indicate whether these fluctuations related mainly to fungal-feeding taxa or whether other feeding groups were involved ? In this connection I might mention that we have found very marked fluctuations in numbers of certain oribatid mite species in woodland soils when different years are compared. Workers may get the impression that apart from seasonal variation the quantitative and qualitative composition of the fauna of a site is relatively static. This impression may result from the practice of studying a site for one year or less. There seems to be a strong case for continuing to sample a site for a longer period than one year where possible.

I. N. HEALEY : Our impression is that wide annual fluctuations are a feature of most of the more abundant fly larval groups in our soils. Fluctuations are especially marked in the Mycetophilidae which appear to be mostly rather general feeders on litter, humus and fungal material, so perhaps they are « opportunistic » forms able to benefit rapidly from short-term changes in the abundance of litter, fungal flora or other potential food supplies. I would strongly endorse Dr MURPHY's emphasis on the need for long-term sampling of soil animal populations.

N. HAARLOV : 1º The other day we discussed the presence of various microorganisms in the gut of soil animals. On the slides, demonstrating the content of the intestines of dipterous larvae we could see hyphae, algae, bacteria, etc. dead and probably alive too. Do you think the larvae digest these organisms, consume their excreta or that they perhaps are of no nutritional importance ? From studies of the digestion of ruminants it is known that the Ciliatae of the rumen are digested by the host and not the bacteria. Have you observed populations of protozoa in the gut of the diptera larvae etc. in separate parts of their intestines ?

2º Have you any information about how long time it will take for a food particle to pass through the gut alone of the dipterous larvae you have studied ?

I. N. HEALEY : 1º I would speculate that the fly larvae probably absorb mostly simple sugars and amino acids that are released from the cell lumen of hyphae, algae, bacteria, etc., as they pass through the gut and are probably also available to some extent in a free form in humus. I suspect that few, if any, of the forms we have been studying are able to break down structural carbonhydrates, but this is pure speculation. We have not observed Protozoa in any number in the guts of fly larvae, although occasional gregarines are seen, as in most arthropods.

2º No, but we are currently working on techniques to enable us to measure this in *Smittia curticosa*.

M. B. BOUCHÉ : Mr. HEALEY a signalé que dans les deux sites les populations larvaires d'*Empididae* et de *Dolichopodidae* sont d'un niveau de densité approximativement semblable. Peut-il fournir quelques indications relatives à une éventuelle similarité des niveaux de populations d'*Enchytraidae*, qui constituent leurs principales proies, dans les deux stations ?

A. RUSSELL-SMITH : We have no figures for enchytraeid populations in the two soils, but on the mull site other workers are carrying out investigations on this group. Our impression is however, that populations are considerably higher in the moder than in the mull soil, despite the fact that level of empidid and dolichopodid populations was similar in the two soils.

P. J. A. HOWARD : I should like to comment on a question concerning variations from year to year aimed at Dr Healey's paper. We have studied weight loss of litter in those successive years, and get curves like figure 3 in shape. However, a dry spell in late February can slow down the weight loss and if this occurs the curve continues in the same shape but the actual values are lower. This means that at the end of a year in which such an early dry spell occurs, the total decomposition is less than if such a dry spell does not occur.